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Niche shift of tephritid species after the Oriental fruit fly (*Bactrocera dorsalis*) invasion in La Réunion

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Abstract

Aim: In a context of successive fruit fly invasions (Tephritidae), this study investigated how the top invader, *Bactrocera dorsalis*, displaced established fruit fly populations. We focused, particularly, on how this invasion impacted the host range and climatic niche of each resident species.

Location: La Réunion, France, Indian Ocean.

Methods: We collected fruit from more than 100 plant species across the island, in cultivated and non-cultivated areas at different altitudes in order to monitor the emergence of fruit flies. Fruit collection was conducted over two field campaigns: from 2001 to 2009, before the *B. dorsalis* invasion; and from 2018 to 2019, after the *B. dorsalis* invasion. We compared the distribution and host range of fruit fly species for the two periods.

Results: Our results confirmed the generalist character of *B. dorsalis*, with the infestation of 52 out of 112 of the fruit species collected in the field. After the *B. dorsalis* invasion, we observed a shift in the host range and spatial distribution of established tephritids. The host range of specialist species that only share a few host species with *B. dorsalis* did not change significantly. On the contrary, we observed a significant shift in diversity or proportion of host range and climatic niches for the generalist species, such as *Bactrocera zonata*, *Ceratitis quilicii* and *Ceratitis capitata*.

Main conclusions: We provide evidence of the competitive displacement induced by *B. dorsalis* on other established species. The coexistence between *B. dorsalis* and generalist *Ceratitis* species seems possible because they have different responses to climatic conditions or the capacity to exploit other host fruit species. In contrast, the coexistence of *B. zonata* with *B. dorsalis* seems to be compromised because both species have similar ecological requirements. This research provides useful information for managing invasions, particularly since understanding competitive displacements is essential for the identification of empty niches and for modelling potential species distribution.

KEYWORDS

Bactrocera zonata, biological invasions, *Ceratitis*, community structure, competitive displacement, fruit fly, host range

1 | INTRODUCTION

Biological invasions are now a major threat to biodiversity (Millennium Ecosystem Assessment (Program), 2005; Murphy & Romanuk, 2014). They can lead to a decrease in gene pools by causing the extinction of native species and alter habitat and ecosystem functions (Simberloff et al., 2013; Vilà et al., 2010). Biological invasions disrupt ecosystem services, such as provisioning services, which also has an important economic impact (Colautti et al., 2006; Olson, 2006; Pimentel et al., 2001; Pimentel, Zuniga, & Morrison, 2005).

Invasive species can interact with established species at different trophic levels. Authors frequently describe interspecific competition, which is widespread among insects and is one of the primary biotic factors that significantly influences their distribution, abundance and diversity in ecological communities (Denno et al., 1995; Reitz & Trumble, 2002). One of the potential outcomes of an interspecific competition event is the competitive displacement of one of the species. DeBach (1966) defined the competitive displacement principle as follows: 'different species having identical ecological niches cannot coexist for long in the same habitat'. The superior competitor can cause the local extinction of the weaker competitor, although this is rare, that is competitive exclusion. In general, the less competitive species uses 'refuge niches', and coexistence continues. Competitive displacement is generally observed between closely related species. In most cases, it is triggered by the invasion of an exotic species, which displaces an indigenous species or an established exotic species (Reitz & Trumble, 2002). Different niche-based hypotheses have attempted to explain mechanisms of successful biological invasions and coexistence. For example, the use of an empty niche by an invader species may reduce competition with native species and allow the coexistence of species. On the contrary, if non-native species are superior competitors, they may compete for resources and cause a niche shift or the competitive exclusion of the native species, which is less common (Amarasekare, 2003; Blonder, 2018; Musseau et al., 2016; Peterson, Rice, & Sexton, 2013; Ricciardi, Hoopes, Marchetti, & Lockwood, 2013). Moreover, the outcome of interspecific competition can be modulated by abiotic conditions, such as temperature and humidity (Rwomushana, Ekesi, Ogol, & Gordon, 2009; Tilman, Mattson, & Langer, 1981). Thus, differential climatic tolerance among competitors can allow species coexistence across environmental gradients (Czárán, 1991).

Duyck and Quilici (2006) define an invasive series as a succession of invasions by closely related taxa in the same territory. In this case, the new invader often replaces the existing species as the dominant species (Duyck et al., 2004; Vila & Weiner, 2004). Invasive series have been observed in the fruit fly community (Diptera: Tephritidae) in La Réunion (Indian Ocean), where nine fruit fly species of economic importance coexist. This community consists of generalist species: *Bactrocera dorsalis*, *B. zonata*, *Ceratitis catoirii*, *C. capitata*, and *C. quilicii*, whose larvae feed on the fruit of various plant families. Furthermore, there are more specialized species, such as *Dacus demmerezi*, *Dacus ciliatus* and *Zeugodacus cucurbitae*, whose larvae feed predominantly on the fruit of Cucurbitaceae; and *Neoceratitis cyanescens*, whose larvae feed on the fruit of the Solanaceae family. Apart from the two endemic species, *C. catoirii* and *D. demmerezi*, fruit flies have successively invaded La Réunion. As far as the generalist species are concerned, *C. capitata* was introduced in 1939 and *C. quilicii* (formerly *Ceratitis rosa*) in 1955. As these species became widespread on the island, the endemic species, *C. catoirii*, became rarer (White, De Meyer, & Stonehouse, 2000). *Bactrocera zonata* invaded La Réunion in 2000. This species became competitively dominant over the other established species, thus, modifying the host range of the other three generalist species (Charlery de la Masselière et al., 2017; Joomaye, Price, & Stonehouse, 2000). A previous study, based on experimental tests of exploitative competition between larvae of *B. zonata*, *C. quilicii*, *C. capitata* and *C. catoirii* showed that the competitive hierarchy of fruit flies reflected their order of invasion (Duyck & Quilici, 2006; Duyck et al., 2004).

Bactrocera dorsalis is the most recent tephritid invader in La Réunion and it was first detected in May 2017. This species is native to India, Southeast Asia and southern China. It is unusually polyphagous and is regarded as one of the top invaders in the world (Clarke et al., 2005). It has spread rapidly throughout Africa. It was first detected in Kenya in 2003 (Lux, Copeland, White, Manrakhan, & Billah, 2003), and has since invaded all countries in sub-Saharan Africa, the Indian Ocean Islands in the Malagasy subregion (De Villiers et al., 2015; Zeng et al., 2019). It was detected in Comoros in 2005, Mayotte in 2007, Madagascar in 2010, Mauritius in 2015 and La Réunion in 2017 (De Meyer et al., 2012; Mauremootoo, Pandoo, Bachraz, Buldowoo, & Cole, 2019). Despite the disastrous economic impact due to loss of fruit production and the associated export markets, the invasion of *B. dorsalis* provides a unique opportunity for observing and evaluating the role of niche differentiation in community assembly in real-time. The impact of *B. dorsalis* on *Ceratitis* species has been observed in other regions, where the dominance of *B. dorsalis* caused a niche displacement but never to the point of extinction because established insect populations were generally maintained in 'refuge niches' (Duyck, Sterlin, et al., 2004; Ekesi, Billah, Nderitu, Lux, & Rwomushana, 2009; Hassani et al., 2016; Mwatawala et al., 2009a, 2009b) . So far, no studies have described the effect of the introduction of *B. dorsalis* on the population dynamics and host range of a resident *B. zonata* population. In La Réunion, the changes in the Tephritidae community caused by the invasion of *B. dorsalis* are hard to predict because they depend on the structure of the invaded community and the invader's competitiveness in specific environmental conditions.

A comparative analysis of interspecific interactions before and after the invasion is necessary to determine how invasive species impact the ecological network. However, few studies include a detailed description of the community structure prior to invasion (Charlery de la Masselière et al., 2017). In La Réunion, this comparison is possible because long-term field databases were compiled from 2001 to 2009 (after *B. zonata*, but before the *B. dorsalis* invasion) and recent data were collected in 2018 (one year after the *B. dorsalis* invasion) and 2019. Drawing on the existing databases, we determined how the top invader, *B. dorsalis*, affected a resident fruit fly community.

We focused on the following points: i) the distribution and host range of this polyphagous species in La Réunion; ii) How the host range has evolved and iii) how the climatic niche of each species changed after this invasion.

2 | METHODS

2.1 | Study site

La Réunion is located in the Southern Indian Ocean (55°30′E; 21°10′S), approximately 700 km off the coast of Madagascar and covers an area of 2 512 km^2. This volcanic island is mountainous, rising to an altitude of 3,100 m, with very rugged topography and a heterogeneous climate. It has a humid tropical climate with two main seasons: a dry season, from May to October, mainly cold and dry with trade winds; and a wet season, from November to April, which is hotter and wetter with light winds. There are two main climatic zones delimited by the central mountain range. The east is exposed to trade winds and has high precipitation (more than 2–3 m per year). In contrast, in the west, the coast is characterized by less humid, even arid, climatic conditions (less than 1 m per year) (Grünberger, 1989).

2.2 | Sampling

We collected fruit samples to monitor Tephritidae infestation in La Réunion. This allowed us to establish a specific link between the host plant and fruit fly species, which is not possible when adult flies are caught with a trap. Agents from CIRAD (a French Agricultural Research Centre for International Development) conducted campaigns from 2001 to 2009. After the invasion of *B. dorsal*is, a further field campaign was conducted in 2018 and 2019. No field collection was conducted between 2009 and 2018. During this period, we consider that the fruit fly community was stable because no new species were introduced (fruit fly and parasitoid species) and the studied abiotic parameters did not change significantly (Appendix S1). Field collection covered the entire island and included cultivated, ornamental and wild plant species. Fruits were randomly collected regardless of the presence or absence of potential punctures. Whenever possible, 15 fruit samples were collected per plant species, site and date. We collected a total of 8,657 individual fruits between 2001 and 2009 in 212 sites, and 10,839 individual fruits in 2018 and 2019 in 172 sites. We collected fruit from 70 potential host plants in the first period and 112 potential host plants in the last period (Table 1). Forty-eight host plant species were the same for both periods.

2.3 | Laboratory rearing of fruit flies

At the end of each day of field sampling, fruits were taken to the laboratory and subjected to a standardized protocol (Boinahadji et al., 2019; FAO/IAEA, 2019; Leblanc, Vueti, Drew, & Allwood, 2012; N'Dépo, My, & Nl, 2019). Fruits were weighed and individually placed in plastic boxes, containing sand as a pupation substrate, and covered with fine-mesh cloth. Fruit samples were kept in a maturation room at 25°C ± 2°C and 70% ± 20% humidity until pupation. These conditions were chosen because they are favourable to the proper development of all fruit fly species of economic importance in La Réunion (Duyck & Quilici, 2002; Duyck, Sterlin, et al., 2004). Over a 3-week period, fruit samples were regularly inspected and the sand was sifted for Tephritidae pupae. Pupae were kept in a climatic room in plastic boxes until emergence. They were taxonomically identified to species level. We collected data on the number of emerging individuals of each fruit fly species for the different fruit (species and weight), site and date. We calculated (a) the infestation rate as the number of fruit fly individuals per kg of collected fruits and (b) the proportion of infested fruit as the number of fruits with at least one fruit fly emergence divided by the number of fruits collected. The proportion of co-infestation was defined as the number of individual fruits with two or more fruit fly species out of the total number of infested fruits.

2.4 | Statistical analysis

Statistical analyses were performed with R version 3.6.2 (R Core Team, 2019). Unless indicated otherwise, data are presented as means ± SE. *Carpomya vesuviana* was only observed once on *Ziziphus mauritiana* and was not included in the following analyses.

2.4.1 | Host range

Only the 48 species that were the same for both periods were kept for analyses (see Appendix S2 for the geographic distribution of samples). For each fruit fly species and each sampling period, the extent of the host niche was calculated as the number of host plant species and by estimating host richness with a Jackknife estimator. Host diversity was also measured with the Shannon index. To estimate changes in the host niche between the first and the second sampling period, we calculated two dissimilarity indexes: Index of Sorensen (Sørensen, 1948), which measures dissimilarity based on presence/absence data (host diversity) and Bray–Curtis (Bray & Curtis, 1957) based on abundance data (host proportion).

We constructed two matrices of interaction between fruit flies and host plant species, one for the historical sampling period (2001–2009) and one for the recent sampling period (2018–2019). For each matrix, rows were normalized by dividing the infestation rate of one fruit fly species for a given host plant species by the global infestation rate of the fruit fly species. We used the 'ggbipart' package to create the bipartite network diagram and the 'FactoMineR' package for the principal component analysis (PCA) from the two interaction matrices.

For each resident species (except *C. catoirii*), we realized a generalized linear mixed model (GLMM) with a negative binomial to test

TABLE 1 Collected plant species in La Réunion in 2018 and 2019 to study the Tephritidae host range

Family	*Latin name*	English name	Status	Weight (g)	*N*
Anacardiaceae	*Anacardium occidentale* L.[a]	Cashew nut	Cultivated	1 166	15
	Mangifera indica L.[a]	Mango	Cultivated	64 049	233
	Spondias dulcis Parkinson[a]	Jew plum	Cultivated	2 431	42
	Spondias mombin L.[a]	Yellow mombin	Cultivated	738	60
Annonaceae	*Annona cherimola* Mill.	Custard apple	Cultivated	36 145	27
	Annona muricata L.[a]	Sursop	Cultivated	4 042	9
	Annona reticulata L.[a]	Bullock's heart	Cultivated	3 622	19
	Cananga odorata (Lam.) Hook. f. & Thomson[a]	Ylang-Ylang	Ornamental	241	60
Aphloiaceae	*Aphloia theiformis* (Vahl) Benn[a]		Endemic	145	45
Apocynaceae	*Carissa carandas* L.	Karanda	Ornamental	186	45
	Cascabela thevetia (L.) Lippold[a]	Yellow oleander	Ornamental	39	106
	Ochrosia borbonica J.F.Gmel.		Endemic	1 936	2
Arecaceae	*Phoenix dactylifera* L.	Date	Naturalized	592	30
Boraginaceae	*Cordia sebestena* L.	Geiger tree	Ornamental	779	90
	Ehretia cymosa Thonn.		Naturalized	2	15
Bromeliaceae	*Ananas comosus* (L.) Merr.[a]	Pineapple	Cultivated	6 808	13
Cactaceae	*Hylocereus undatus* (Haw.) Britton & Rose[a]	Dragon fruit	Cultivated	4 706	13
	Opuntia ficus-indica (L.) Miller	Sweet prickly pear	Naturalized	1 558	35
Caricaceae	*Carica papaya* L.[a]	Papaya	Cultivated	19 931	35
Chrysobalanaceae	*Chrysobalanus icaco* L.[a]	Coco plum	Cultivated	216	15
Clusiaceae	*Calophyllum inophyllum* L.[a]	Alexandrian Laurel	Ornamental	997	30
Clusiaceae	*Garcinia xanthochymus* Hook.f.[a]	False mangosteen	Cultivated	900	8
Combretaceae	*Terminalia catappa* L.[a]	Indian almond	Ornamental	19 382	588
Cucurbitaceae	*Coccinia grandis* (L.) Voigt.[a]	Ivy gourd	Invasive (5)	1 275	105
	Cucumis sativus L.[a]	Cucumber	Cultivated	2 192	15
	Cucurbita moschata Duchesne[a]	Pumpkin	Cultivated	870	51
	Cucurbita pepo L.[a]	Zucchini squash	Cultivated	2 561	30
	Lagenaria siceraria (Molina) Standl.[a]	Bottle gourd	Cultivated	4 486	16
	Lagenaria sphaerica (Sond.) Naudin	Wild melon	Naturalized	3 750	10
	Momordica charantia L.[a]	Bitter gourd	Invasive (5), Cultivated	3 560	295
	Sechium edule (Jacq.) Sw.[a]	Chayote	Invasive (4), Cultivated	22 842	118
Ebenaceae	*Diospyros blancoi* A.DC.[a]	Velvet apple	Cultivated	3 423	30
	Diospyros kaki L. f.[a]	Persimmon	Cultivated	10 457	135
	Diospyros nigra (J.F.Gmel.) Perrier[a]	Black sapote	Invasive (4), Cultivated	5 603	60
Euphorbiaceae	*Jatropha curcas* L.	Pignut	Naturalized	198	15
Fabaceae	*Inga laurina* (Sw.) Willd.[a]	Sackycac	Cultivated	691	30
	Pithecellobium dulce (Roxb.)[a]	Guamuchil apes-earring	Naturalized	275	30

(Continues)

TABLE 1 (Continued)

Family	*Latin name*	English name	Status	Weight (g)	*N*
Goodeniaceae	*Scaevola taccada* (Gaertn.) Roxb.[a]	Beach naupaka	Indigena	199	145
Lauraceae	*Persea americana* Mill.[a]	Avocado	Cultivated	23 815	73
Laureae	*Litsea glutinosa* (Lour.) C.B.Rob.	Indian laurel	Invasive (5)	44	30
Lythraceae	*Punica granatum* L.	Pomegranate	Cultivated	2,175	16
Malpighiaceae	*Bunchosia armeniaca* (Cav.) DC.	Peanut Butter Fruit	Ornamental	282	30
Melastomataceae	*Clidemia hirta* (L.) D. Don	Koster's curse	Invasive (5)	16.9	30
Meliaceae	*Azadirachta indica* A.Juss.	Neem	Naturalized	540	30
Monnimiaceae	*Tambourissa elliptica* (Tul.) A. DC.		Endemic	302	15
Moraceae	*Artocarpus altilis* (Parkinson) Fosberg	Breadfruit	Cultivated	886	1
	Ficus benghalensis L.	Banyan	Ornamental	37	15
	Ficus carica L.[a]	Fig	Cultivated	1 910	60
	Ficus lateriflora Vahl.[a]		Endemic	100	15
	Ficus mauritiana Lam.[a]		Endemic	1 856	30
	Ficus pumila L.	Creeping Fig	Naturalized	1 506	60
	Ficus sycomorus L.	Sycamore Fig	Cultivated	80	15
Musaceae	*Musa acuminata* Colla	Banana	Cultivated	6 751	64
Myrtaceae	*Eugenia brasiliensis* Lamarck[a]	Spanish cherry	Naturalized	44	15
	Eugenia uniflora L.	Brasilian cherry	Naturalized	546	120
	Plinia cauliflora (Mart.)	Jabuticaba	Cultivated	198	30
	Psidium catlleianum Sabine[a]	Strawberry guava	Invasive (5), Cultivated	15 886	1,041
	Psidium guajava L.[a]	Common guava	Cultivated	28 709	550
	Syzygium cumini (L.) Skeels	Java plum	Invasive (4)	346	75
	Syzygium cymosum (Lam.) DC.[a]		Endemic	386	38
	Syzygium jambos (L.) Alston[a]	Rose-apple	Invasive (5)	11 028	570
	Syzygium malaccense (L.) Merr. & L. M. Perry[a]	Malay apple	Naturalized	917	25
	Syzygium samarangense (Blume) Merr. & L. M. Perry[a]	Java apple	Naturalized	3 322	165
Oleaceae	*Ligustrum sp.*	Privet	Invasive (4)	1	15
	Noronhia emarginata (Lam.) Thouars[a]	Madagascar olive	Naturalized	632	30
Onagraceae	*Fuchsia boliviana* Carrière	Bolivian fuchsia	Invasive (5)	17	15
Oxalidaceae	*Averrhoa bilimbi* L.[a]	Cucumber tree	Cultivated	1 632	55
	Averrhoa carambola L.[a]	Star fruit	Cultivated	4 402	63
Passifloraceae	*Passiflora edulis* Sims	Passionfruit	Naturalized	1 803	30
	Passiflora foetida L.	Wild maracuja	Naturalized	60	30
	Passiflora molissima (Kunth) L.H.Bailey[a]	Banana passionfruit	Invasive (5)	2 614	60
	Passiflora quadrangularis L.	Giant Granadilla	Cultivated	91	1
	Passiflora sp.[a]	Passionfruit	Naturalized	900	15

(Continues)

TABLE 1 (Continued)

Family	*Latin name*	English name	Status	Weight (g)	*N*
	Passiflora suberosa L.[a]	Corkystem passionflower	Invasive (4)	142	96
Phytolaccaceae	*Phytolacca americana* L.	Pokeweeds	Naturalized	24	30
Polygonaceae	*Coccoloba uvifera* L.[a]	Seagrape	Naturalized	268	60
Primulaceae	*Ardisia crenata* Sims	Christmas berry	Naturalized	35	1
Rhamnaceae	*Ziziphus mauritiana* Lamarck[a]	Indian jujube	Cultivated	2 428	105
Rosaceae	*Eriobotrya japonica* (Thunb.) Lindley[a]	Loquat	Invasive (5)	4 481	359
	Malus pumila Borkh.[a]	Apple tree	Cultivated	1 016	23
	Prunus persica (L.) Batsch[a]	Peach tree	Cultivated	10 008	268
	Prunus sp. L.[a]	Plum tree	Cultivated	3 789	83
	Pyrus sp. L.[a]	Pear	Cultivated	7 669	78
Rubiaceae	*Bertiera rufa* DC.		Endemic	2	15
	Coffea sp.L.[a]	Coffee	Cultivated	885	193
	Gaertnera vaginata Lam.		Endemic	24	14
Rutaceae	*Citrus aurantifolia* (Christm.) Swing. *x Fortunella* sp.[a]	Limequat	Cultivated	5 613	11
	Citrus clementina Hort. ex Tan.[a]	Clementine	Cultivated	648	80
	Citrus limon (L.) Burm. f.	Lemon tree	Cultivated	1 196	3
	Citrus maxima (Burm.) Merr.		Cultivated	702	1
	Citrus paradisi Macfad.	Grapfruit	Cultivated	1 956	2
	Citrus reticulata Blanco	Mandarin tree	Cultivated	5 732	30
	Citrus reticulata Blanco x *Citrus sinensis* (L.) Osb.[a]	Tangor	Cultivated	9 230	51
	Citrus sinensis (L.) Osbeck[a]	Orange tree	Cultivated	6 281	75
	Citrus tangerina Hort. ex Tan.[a]		Cultivated	354	104
	Murraya paniculata (L.) Jacq.[a]	Jessamine orange	Invasive (4), Ornamental	149	120
Salicaceae	*Dovyalis hebecarpa* (Gardner) Warburg[a]	Ceylon gooseberry	Cultivated	397	45
	Flacourtia indica (Burman f.) Merrill[a]	Governor's plum	Ornamental	920	108
Sapindaceae	*Dimocarpus longan* Lour.	Longan	Cultivated	230	30
	Litchi chinensis Sonnerat[a]	Litchi	Cultivated	1 071	181
Sapotaceae	*Chrysophyllum cainito* L.[a]	Star-apple	Cultivated	1 222	15
	Labourdonnaisia calophylloides Bojer		Endemic	12	1
	Mimusops coriacea (A.DC.) Miq.[a]	Monkey's apple	Ornamental	2 497	75
	Mimusops elengi L.[a]	Spanish cherry	Cultivated	287	59
	Sideroxylon borbonicum DC.		Endemic	2	7
Solanaceae	*Capsicum frutescens* L.[a]	Chilli	Cultivated	318	73
	Solanum betaceum Cav.[a]	Tomato tree	Cultivated	2 705	56
	*Solanum lycopersicum*L.[a]	Tomato	Cultivated	2 075	91
	Solanum mauritianum Scop.[a]	Bugweed	Invasive (5)	940	270
	Solanum melongena L.[a]	Eggplant	Cultivated	3 289	27

(Continues)

TABLE 1 (Continued)

Family	*Latin name*	English name	Status	Weight (g)	*N*
	Solanum nigrum L.[a]	Black nightshade	Naturalized	17	32
	Solanum torvum Sw.[a]	Turkey berry	Naturalized	94	30

[a]Fruit fly host plant species. The level of invasion according to Lavergne, 2016, is presented into brackets in the status column: (4) moderately invasive exotic species in more or less important densities; spreading in natural, semi-natural and anthropized environments, without however dominating vegetation and with a moderate impact on native ecosystems; (5): very invasive exotic species: wide spatial distribution, very numerous populations, high densities; dominant or co-dominant in both anthropogenic, semi-natural and natural environments, and exerting a significant direct impact on native ecosystems. *N*: Number of collected samples.

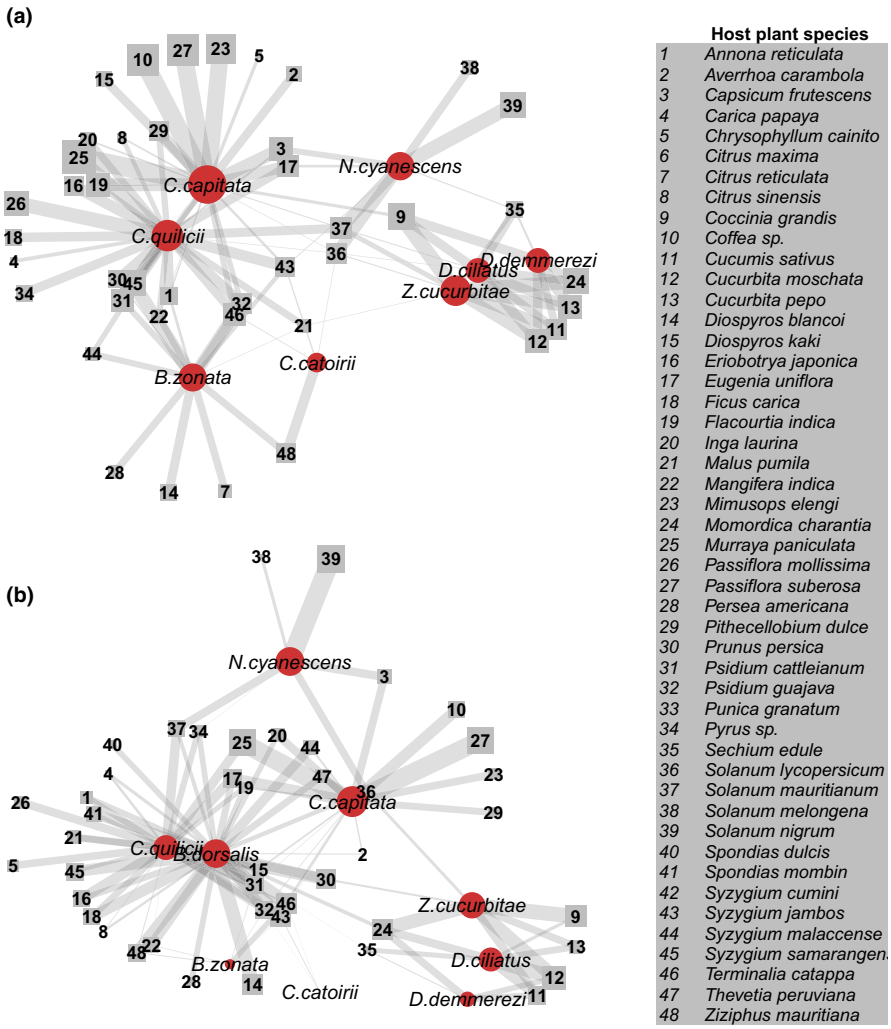

FIGURE 1 Bipartite network diagram showing interactions between fruit fly species and host plant species from 2001 to 2009 (a) and in 2018 and 2019 (b) in La Réunion. The width of nodes and links is proportional to the number of flies/kg of fruit. Nodes placement was realized according to Fruchterman–Reingold force-directed algorithm

the effect of the studied period on the infestation rate. Host plant species, seasons (winter or summer), and sites were added as random factors.

2.4.2 | Climatic range

Climatic data (maps with mean annual temperature and mean annual precipitation) were drawn from the AWARE Atlas (https://smartis.re/p/AWARE), which was developed by CIRAD in La Réunion. We used precipitation and temperature as environmental predictors. These factors impact fly development (Eskafi & Fernandez, 1990; Mahmoud, 2016; Shoukry & Hafez, 1979; Teruya, 1990; Vargas, Walsh, Jang, Armstrong, & Kanehisa, 1996; Yang, Carey, & Dowell, 1994) and, therefore, influence the distribution and abundance of Tephritidae (De Villiers et al., 2015; Duyck, et al., 2004; Ni et al., 2012). Extrapolated temperature data were derived from 73 meteorological stations evenly distributed across La Réunion and collected between 1997 and 2017. Precipitation data were obtained from 143 stations and collected between 1986 and 2016 by Météo-France and CIRAD. Prior to the analysis of climatic niches, we analysed data from METEOR (https://smartis.re/METEOR) to verify the absence of climatic changes between the two studied periods. METEOR provides information on daily temperature, precipitation

and solar radiation. We selected data for 30 sites in 10 different municipalities and for three different elevation ranges (0–300 m; 301–600 m and > 600 m), and compared mean values for the two studied periods (Appendix S1).

We only studied the climatic range for generalist fruit fly species because of the uneven distribution of the host fruit of specialist species (Cucurbitaceae and Solanaceae). To study the distribution of each fruit fly species, we reduced the data set and focused on host fruit with high infestation rates and broad distribution across the island. We kept data from: *Prunus persica*, *Psidium cattleianum*, *Psidium guajava*, *Syzygium jambos* and *Terminalia catappa* for *B. dorsalis*, *B. zonata*, *C. quilicii* and *C. catoirii*; and data from *Eugenia uniflora*, *Murraya paniculata*, *Passiflora suberosa* and *T. catappa* for *C. capitata*.

For each fruit fly species and each studied period, we used a generalized linear mixed model with negative binomial distribution to test the influence of temperature and precipitation on the infestation rate. Host plant species, seasons (winter or summer), and sites were added as random factors.

For each fruit fly species, a niche comparison between the two studied periods was performed using the 'ecospat' package (Cola et al., 2017). Niche functions in the 'ecospat' package provide tools to quantify and compare species niches with an ordination approach. Niche was described in relation to precipitation and temperature. The global overlap between niches was calculated using metrics of Schoener's D or Hellinger's I, ranging from 0 (no overlap) to 1 (complete overlap)(Broennimann et al., 2012). We performed tests of niche equivalency and similarity. The niche equivalency test assesses, through 1,000 random permutations of occurrences between ranges, whether the two niches are equivalent. The niche similarity test assesses, through 1,000 random shifts of the niches within available conditions in the study area, whether the species niches are more or less similar than expected by chance.

3 | RESULTS

3.1 | Tephritidae community structure

Among the nine tephritid species analysed in this study, three were found mostly on Cucurbitaceae (*D. ciliatus*, *D. demmerezi* and *Z. cucurbitae*), one mostly on Solanaceae (*N. cyanescens*) and the others (*B. zonata*, *C. capitata*, *C. catoirii*, *C. quilicii* and after 2017, *B. dorsalis*) on plants from various families (Figure 1). During the first studied period, the generalist species, *C. quilicii* and *C. capitata*, had a close host niche and shared 18 host plant species. *Bactrocera zonata* shared 10 species with *C. quilicii* and 8 with *C. capitata* before 2017 (Figure 1a). After the *B. dorsalis* invasion, we observed several modifications in the network configuration: *C. quilicii* and *C. capitata* shared only eight host plant species, while *B. dorsalis* had a host niche that was very close to that of *C. quilicii* and shared 20 host plant species. All seven host plant species infested by *B. zonata* were shared with both *C. quilicii* and *B. dorsalis* in 2018–2019 (Figure 1b).

On infested fruit, 18.9% of samples hosted two or more species (co-infestation) in 2001–2009 and 9.5% in 2018–2019. For example, we observed a decrease in co-infestation in *B. dorsalis*' main fruit hosts: from 23.3% to 10.4% for *Mangifera indica*, from 24.4% to 10.3% for *Psidium guajava* and from 28.1% to 11.1% for *Terminalia catappa*. In 2001–2009, data for co-infested fruits reveals that 35% were infested simultaneously by *B. zonata/C. quilicii*, 16% by *Z. cucurbitae/D. ciliatus*, *16% by C. capitata/C. quilicii*, 8% by *Z. cucurbitae/D. demmerezi*, 6% by *Z. cucurbitae/D. ciliatus/D. demmerezi* and 6% by *B. zonata/C. capitata/C. quilicii*. In 2018–2019, 68% of co-infested fruit was simultaneously infested by *B. dorsalis/C. quilicii*, 11% by *B. dorsalis/B. zonata and 5% by Z. cucurbitae/D. ciliatus*.

3.2 | Host range

The principal component analysis (PCA, Figure 2) allowed us to determine specific host plant species of fruit flies in 2001–2009 and 2018–2019. According to axis 1 (Figure 2a,c), *C. quilicii* and *B. dorsalis* host diversity was high and included many species, such as *Annona reticulata*, *Carica papaya*, *Eriobotrya japonica*, *Eugenia uniflora*, *Ficus carica*, *Malus pumila*, *Pyrus* sp. and *P. catlleianum*. Axis 2 (Figure 2b,d) shows that *C. capitata's* host diversity included *Coffea* sp., *Mimusops elengi*, *Murraya paniculata*, *Passiflora suberosa* and *Pithecellobium dulce*. Axis 3 (Figure 2b.d) distinguishes *B. dorsalis* and *B. zonata* (2001–2009) host range according to *Citrus reticulata*, *Diospyros blancoi*, *Persea americana*, *Syzygium malaccence* and *Syzygium samarangense*. *Dacus ciliatus*, *D. demmerezi*, and *Z. cucurbitae* have very similar host diversity. Moreover, the PCA revealed differences in host diversity between the two studied periods for generalist but not specialist species.

3.2.1 | *Bactrocera dorsalis*

Among the 112 potential host plant species sampled, 52 were infested by *B. dorsalis* (Table 2). This tephritid was found in fruit from many cultivated species of economic importance in La Réunion, such as *Ananas comosus* (23.1% infested fruit, 1.5 flies/kg, $N = 13$), *Carica papaya* (5.7% of infested fruit, 2.1 flies/kg, $N = 35$), *Hylocereus undatus* (76.9% of infested fruit, 43.1 flies/kg, $N = 13$), *Litchi chinensis* (1.66% of infested fruit, 1.34 flies/kg, $N = 181$), *Mangifera indica* (45.5% of infested fruit, 38.4 flies/kg, $N = 233$) or *Musa sp.* (32.8% infested fruit, 62.4 flies/kg, $N = 64$). Some species in gardens and urban areas had high infestation rates, for example, *Anacardium occidentale* (73.3% infested fruit, 73.8 flies/kg, $N = 15$), *Chrysobalanus icaco* (60% infested fruit, 124.9 flies/kg, $N = 15$), *Diospyros blancoi* (43.3% infested fruit, 139.7 flies/kg, $N = 30$) or *Terminalia catappa* (43.5% infested fruit, 131.8 flies/kg, $N = 588$). This species also infested naturalized and invasive species, such as *Syzygium jambos* (44.2% infested fruit, 140.7 flies/kg, $N = 570$), *Syzygium samarangense* (29.7% infested fruit, 61.4 flies/kg, $N = 165$) or *Psidium cattleianum* (27.3% infested fruit, 67.4 flies/

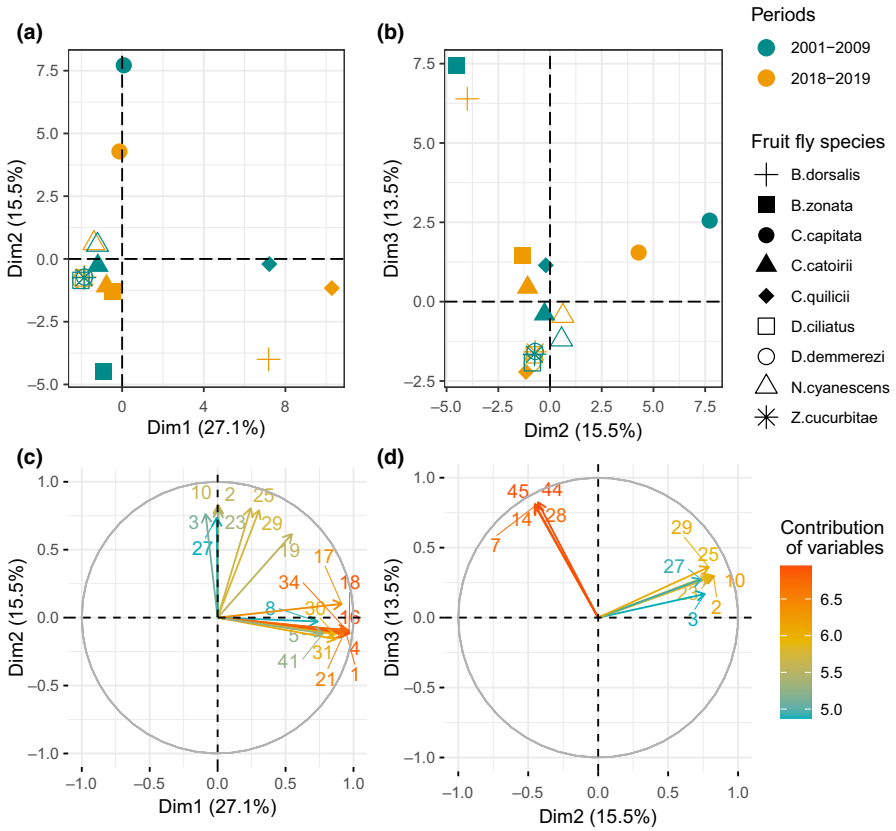

FIGURE 2 Individuals (a, b) and variables (c, d) plot of principal component analysis showing fruit fly species according to their host diversity (proportion of each plant species in the host range) in La Réunion. Vectors indicate the direction and strength of each host plant species (only variables with cos2 superior to 0.5 were represented). See Figure 1 for number correspondence

kg, $N = 1{,}041$). Lastly, some endemic species were also infested by *B. dorsalis*, such as *Ficus lateriflora* (13.3% infested fruit, 19.9 flies/kg, $N = 15$) or *Aphloia theiformis* (8.9% infested fruit, 27.6 flies/kg, $N = 45$, Table 2). Although *B. dorsalis* preferred sweet fruit, we observed a slight infestation on samples from the Curcubitaceae and Solanaceae families, such as *Momordica charantia* (0.7% infested fruit, 2.8 flies/kg, $N = 295$), *Sechium edule* (1.7% infested fruit, 0.1 flies/kg, $N = 118$), *Solanum betaceum* (1.8% infested fruit, 0.4 flies/kg, $N = 56$), and *Solanum lycopersicum* (1.1% infested fruit, 3.9 flies/kg, $N = 91$).

3.2.2 | *Bactrocera zonata*

Diversity and richness of *B. zonata's* host range were reduced by half after the *B. dorsalis* invasion and only seven host plant species were detected in 2018–2019 (Table 3). Jackknife estimation of species richness decreased from 16.0 ± 1.4 in 2001–2009 to 12.0 ± 2.2 in 2018–2019.

The dissimilarity indexes of Bray–Curtis (0.98) and Sorensen (0.65) suggested that the host range (diversity and proportion of species) changed between the two periods. Of the 15 species in *B. zonata's host range*, six were the same for both sampling periods. In 2001–2009, *B. zonata's* host diversity was characterized by *C. reticulata*, *D. blancoi*, *P. americana*, *S. malaccence* and *S. samarangense* (Figures 1a, 2). In 2018–2019, these species were absent from its host range and *T. catappa* was the main host plant species (Figure 1b).

We also observed a significant decrease in the infestation rate of selected host plant species *(P. persica*, *P. cattleianum*, *P. guajava*, *S. jambos and T. catappa)* between the two periods from 91.20 ± 4.89 fruit flies/kg to 1.33 ± 0.32 fruit flies/kg ($Z = 5.403$; $p < .001$).

3.2.3 | *Ceratitis quilicii*

The species richness of the host range was similar for the two periods (Table 3). Jackknife estimation of species richness was 28.0 ± 2.0 in 2001–2009 and 29.0 ± 2.4 in 2018–2019.

The dissimilarity indexes of Bray–Curtis (0.66) and Sorensen (0.44) suggested that the host niche changed (in terms of diversity and proportion of species) between the two periods. Of the 28 species in *C. quilicii's* host range, 18 were the same for both sampling periods.

In 2001–2009, *P. cattleianum*, *M. panicalata* and *P. mollissima* were important host plant species of *C. quilicii* in terms of infestation rate (Figure 1a). In 2018–2019, *P. persica* and *E. japonica* were the main host plant species (Figure 1b).

We also observed a significant decrease in the infestation rate of selected host plant species *(P. persica*, *P. cattleianum*, *P. guajava*, *S. jambos and T. catappa)* between the two periods from 73.80 ± 3.13 fruit flies/kg to 23.86 ± 1.54 fruit flies/kg ($\chi^2_1 = 6.092$; $p = .014$).

TABLE 2 Fruit fly emergence according to host plants collected in 2018 and 2019 in La Réunion

Family	*Latin name*	*N*	*Pupae*	*B.d*		*B.z*		*C.cap*		*C.qui*		*C.cat*		*Z.c*		*D.c*		*D.d*		*N.c*	
			b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
Anacardiaceae	*Anacardium occidentale*	15	114.1	73.3	73.8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Mangifera indica	233	69.5	45.5	38.4	3.4	0.3	.	.	1.3	0.1	.	.	.	.	.	.	.	.	.	.
	Spondias dulcis	42	17.3	7.1	7.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Spondias mombin	60	59.6	15.0	39.3	.	.	.	.	1.7	4.1	.	.	.	.	.	.	.	.	.	.
Annonaceae	*Annona muricata*	9	4.7	11.1	0.2	.	.	.	.	11.1	2.7	.	.	.	.	.	.	.	.	.	.
	Annona reticulata	19	18.2	5.3	7.2	.	.	.	.	10.5	9.7	.	.	.	.	.	.	.	.	.	.
	Cananga odorata	60	95.3	8.3	53.9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aphloiaceae	*Aphloia theiformis*[1]	45	62.2	8.9	27.6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Apocynaceae	*Cascabela thevetia*	106	46.0	5.7	10.8	.	.	1.9	11.9	.	.	.	.	.	.	.	.	.	.	.	.
Arecaceae	*Phoenix dactylifera*	30	1.7	3.3	1.7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bromeliaceae	*Ananas comosus*[1]	13	2.6	23.1	1.5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cactaceae	*Hylocereus undatus*	13	62.9	76.9	43.1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Caricaceae	*Carica papaya*	35	7.6	5.7	2.1	.	.	.	.	14.3	1.6	.	.	.	.	.	.	.	.	.	.
Chrysobalanaceae	*Chrysobalanus icaco*[1]	15	365.4	60	124.9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Clusiaceae	*Calophyllum inophyllum*	30	30.0	3.3	2.0	.	.	3.3	1.0	.	.	.	.	.	.	.	.	.	.	.	.
	Garcinia xanthochymus[1]	8	70.0	37.5	35.6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Combretaceae	*Terminalia catappa*	588	291.9	43.5	131.8	4.6	6.0	1.2	1.4	2.0	1.3	0.2	0.1	.	.	.	.	.	.	.	.
Cucurbitaceae	*Coccinia grandis*	105	317.7	.	.	.	.	.	.	.	.	.	.	41.0	201.6	1.0	2.4	.	.	.	.
	Cucumis sativus	15	86.2	.	.	.	.	.	.	.	.	.	.	33.3	17.8	53.3	53.4	13.3	9.1	.	.
	Cucurbita moschata	51	600.9	.	.	.	.	.	.	.	.	.	.	33.3	147.7	35.3	189.1	7.8	6.7	.	.
	Cucurbita pepo	30	26.9	.	.	.	.	.	.	.	.	.	.	3.3	12.9	13.3	10.5	.	.	.	.
	Lagenaria siceraria	16	14.7	.	.	.	.	.	.	.	.	.	.	6.3	6.7	.	.	12.5	3.1	.	.
	Momordica charantia	295	311.5	0.7	2.8	.	.	.	.	.	.	.	.	28.5	134.6	6.8	18.5	5.8	12.9	.	.

(Continues)

TABLE 2 (Continued)

Family	Latin name	N	Pupae	B.d		B.z		C.cap		C.qui		C.cat		Z.c		D.c		D.d		N.c	
			b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
	Sechium edule[1]	118	8.9	1.7	0.1	.	.	.	.	.	.	.	.	.	.	12.7	5.0	2.5	0.5	.	.
Ebenaceae	*Diospyros blancoi*[1]	30	247.2	43.3	139.7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Diospyros kaki	135	26.1	14.8	9.2	0.7	0.1	0.7	0.9	4.4	2.5	.	.	.	.	.	.	.	.	.	.
	Diospyros nigra[1]	60	2.3	3.3	1.1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Fabaceae	*Inga laurina*[1]	30	28.9	3.3	5.8	.	.	10	17.4	.	.	.	.	.	.	.	.	.	.	.	.
	Pithecellobium dulce	30	10.9	.	.	.	.	3.3	10.9	.	.	.	.	.	.	.	.	.	.	.	.
Lauraceae	*Persea americana*	73	9.1	11.0	6.9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Moraceae	*Ficus carica*	60	159.7	30	49.2	.	.	.	.	15.0	10.5	.	.	.	.	.	.	.	.	.	.
	Ficus lateriflora[1]	15	19.9	13.3	19.9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Ficus mauritiana	30	16.7	.	.	.	.	.	.	6.7	11.9	.	.	.	.	.	.	.	.	.	.
Musaceae	*Musa acuminata*	64	93.6	32.8	62.4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Myrtaceae	*Eugenia uniflora*	120	192.2	4.2	11.0	.	.	13.3	47.6	6.7	34.8	.	.	.	.	.	.	.	.	.	.
	Psidium catlleianum	1,041	177.2	27.3	67.4	0.2	0.3	0.2	0.2	15.7	26.2	.	.	.	.	.	.	.	.	.	.
	Psidium guajava	550	120.8	19.3	46.2	0.4	0.2	0.5	0.3	22.7	16.1	0.2	0.1	.	.	.	.	.	.	.	.
	Syzygium jambos	570	305.1	44.2	140.7	0.4	0.2	0.4	0.2	15.3	22.1	0.5	0.4	.	.	.	.	.	.	.	.
	Syzygium malaccense	25	36.0	20	30.5	.	.	4.0	1.1	.	.	.	.	.	.	.	.	.	.	.	.
	Syzygium samarangense	165	115.6	29.7	61.4	.	.	.	.	4.8	3.6	.	.	.	.	.	.	.	.	.	.
Oleaceae	*Noronhia emarginata*[1]	30	4.7	3.3	1.6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Oxalidaceae	*Averrhoa bilimbi*	55	0.6	1.8	0.6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Averrhoa carambola	63	1.8	1.6	0.5	.	.	3.2	0.7	.	.	.	.	.	.	.	.	.	.	.	.
Passifloraceae	*Passiflora molissima*	60	62.7	.	.	.	.	.	.	23.3	18.0	.	.	.	.	.	.	.	.	.	.
	Passiflora suberosa	96	993.3	.	.	.	.	43.8	746.7	.	.	.	.	.	.	.	.	.	.	.	.
Polygonaceae	*Coccoloba uvifera*[1]	60	11.2	5.0	11.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

(Continues)

TABLE 2 (Continued)

Family	*Latin name*	*N*	*Pupae*	*B.d*		*B.z*		*C.cap*		*C.qui*		*C.cat*		*Z.c*		*D.c*		*D.d*		*N.c*	
			b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
Rhamnaceae	*Ziziphus mauritiana*	105	97.6	25.7	68.8	1.0	0.4	.	.	1.0	0.4	.	.	.	.	.	.	.	.	.	.
Rosaceae	*Eriobotrya japonica*	359	153.6	5.0	9.2	.	.	.	.	22.6	42.0	.	.	.	.	.	.	.	.	.	.
	Malus pumila	23	46.3	17.4	10.8	.	.	.	.	13.0	11.8	.	.	.	.	.	.	.	.	.	.
	Prunus persica	268	221.4	26.9	34.8	.	.	.	.	45.1	69.6	.	.	.	.	.	.	.	.	.	.
	Prunus sp.	83	108.2	7.2	6.9	.	.	.	.	38.6	33.2	.	.	.	.	.	.	.	.	.	.
	Pyrus sp.	78	42.2	12.8	6.5	.	.	.	.	25.6	8.2	.	.	.	.	.	.	.	.	.	.
Rubiaceae	*Coffea* sp.	193	65.7	.	.	.	.	14.0	53.0	.	.	.	.	.	.	.	.	.	.	.	.
Rutaceae	*Citrus aurantifolia. x Fortunella* sp.	11	62.1	36.4	48.0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Citrus clementina	80	2.3	.	.	.	.	.	.	1.3	0.2	.	.	.	.	.	.	.	.	.	.
	Citrus reticulata x Citrus sinensis	51	6.8	.	.	.	.	.	.	9.8	3.1	.	.	.	.	.	.	.	.	.	.
	Citrus sinensis	75	2.3	9.3	1.4	.	.	.	.	2.7	0.3	.	.	.	.	.	.	.	.	.	.
	Citrus tangerina	104	3.8	.	.	.	.	.	.	1.9	0.6	.	.	.	.	.	.	.	.	.	.
	Murraya paniculata	120	1,137.5	.	.	.	.	44.2	789.6	3.3	26.8	.	.	.	.	.	.	.	.	.	.
Salicaceae	*Dovyalis hebecarpa*[1]	45	37.8	4.4	10.1	.	.	.	.	2.2	2.5	.	.	.	.	.	.	.	.	.	.
	Flacourtia indica[1]	108	31.5	0.9	5.4	.	.	0.9	1.1	3.7	5.4	.	.	.	.	.	.	.	.	.	.
Sapindaceae	*Litchi chinensis*	181	1.6	1.7	1.3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sapotaceae	*Chrysophyllum cainito*	15	27.8	.	.	.	.	.	.	20	13.9	.	.	.	.	.	.	.	.	.	.
	Mimusops coriacea[1]	75	9.2	4.0	5.6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Mimusops elengi	59	13.9	.	.	.	.	1.7	13.9	.	.	.	.	.	.	.	.	.	.	.	.
Solanaceae	*Capsicum frutescens*	73	47.2	.	.	.	.	4.1	15.7	.	.	.	.	.	.	.	.	.	.	6.8	18.9
	Solanum betaceum[1]	56	9.2	1.8	0.4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3.6	6.7
	Solanum lycopersicum	91	24.1	1.1	3.9	.	.	1.1	0.5	.	.	.	.	.	.	.	.	.	.	13.2	13.0

(Continues)

TABLE 2 (Continued)

Family	Latin name	N	Pupae	B.d		B.z		C.cap		C.qui		C.cat		Z.c		D.c		D.d		N.c	
			b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
	Solanum mauritianum	270	77.6	0.4	3.2	.	.	.	.	4.1	29.8	.	.	.	.	.	.	.	.	3.0	18.1
	Solanum melongena	27	6.1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	14.8	2.1
	Solanum nigrum	32	681.8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	31.3	606.1
	Solanum torvum	30	85.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	13.3	74.5

Note: a: percentage of infested fruits, b: Fruit fly number/ kg of fruit,
B.d: Bactrocera dorsalis, *B.z: Bactrocera zonata*, *C. cap: Ceratitis capitata*, *C.qui: Ceratitis quilicii*, *C.cat: Ceratitis. catoirii*, *Z.c: Zeugodacus cucurbitae*, *D.c: Dacus ciliatus*, *D.d: Dacus demmerezi*, *N.c: Neoceratitis cyanescens*.
N: Number of collected samples.
[1]New host plant for *B. dorsalis* according to the following literature: Badii et al. (2015), Billah and Ekesi (2006), Boinahadji et al. (2019), De Meyer et al. (2014), Fadlelmula and Ali (2014), K. Geurts, Mwatawala, and De Meyer (2014), Goergen et al. (2011), Gomina (2015), Hassani (2017), Isabirye et al. (2016), Iwaizumi (2004), José, Cugala, and Santos (2013), Leblanc, Vueti, and Allwood (2013), McQuate (2010), Mwatawala, De Meyer, Makundi, and Maerere (2006, 2009b), Mziray, Makundi, Mwatawala, Maerere, and De Meyer (2010), N'Dépo et al. (2010), Ndiaye et al. (2012), Rattanapun (2009), Rwomushana, Ekesi, Gordon, and Ogol (2008), Theron, Manrakhan, and Weldon (2017), Vargas, Leblanc, Putoa, and Eitam (2007), Vayssières, Sinzogan, and Adandonon (2009), I.M. White and Elson-Harris (1992).

3.2.4 | *Ceratitis capitata*

Host range species richness was similar for the two periods (Table 3). Jackknife estimation of species richness was 32.0 ± 2.6 in 2001–2009 and 29.0 ± 3.3 in 2018–2019.

The dissimilarity index of Bray–Curtis (0.67) and Sorensen (0.51) suggested a shift in host range (in terms of diversity and proportion of species) between the two periods. Of the 27 species in *C. capitata's* host range, 16 were the same for both sampling periods. Moreover, of the five characteristic species observed in 2001–2009, only *M. paniculata* and *P. suberosa* were very important host plant species in 2018–2019 (Figure 2). They represent 90% of infestations (fruit flies/kg, Figure 1b). *Coffea* sp., *M. elengi* and *P. dulce* were host plants in both periods, but the proportion of infested fruits was lower in 2018–2019.

We also observed a significant decrease in the infestation rate of selected host plant species *(Coffea* sp., *E. uniflora*, *M. paniculata*, *P. suberosa*, *T. catappa)* between the two periods ($\chi^2_1 = 17.504$; $p < .001$) from 157.85 ± 10.02 fruit flies/kg to 43.20 ± 16.57 fruit flies/kg.

3.2.5 | *Ceratitis catoirii*

This rare endemic species was only observed in 77 fruits (of the 6,929 fruit samples collected, vegetables excluded) between 2001 and 2009 and in 5 fruits (of a total of 8,276 fruit samples, vegetables excluded) in 2018–2019. The species richness of the host range was similar for the two periods (Table 3). Jackknife estimation of species richness was 7.0 ± 1.4 in 2001–2009 and 5.0 ± 1.4 in 2018–2019. *Ceratitis catoirii* was mainly observed in *Z. mauritiana* during the first sampling period and in *T. catappa* during the second sampling period (Figure 1).

3.2.6 | Other Tephritidae species

Diversity and species richness of the host range was similar for the two periods for *D. ciliatus*, *D. demmerezi*, *Z. cucurbitae* and *N. cyanescens* (Table 3, Figure 1a, 1b). Nevertheless, we observed some differences in host niche in terms of diversity and proportion of species (Bray–Curtis: 0.29–0.84 and Sorensen: 0.38–0.50), probably due to the lower host diversity.

3.3 | Geographic and climatic distribution

3.3.1 | *Bactrocera dorsalis*

One year after it was first detected, *B. dorsalis* was found all over the island, at a range of from 0 to 1 600 m, the maximal altitude sampled (Figures 3a and 4a). The number of flies per kg significantly increased with temperature (Z = 3.124; $p = .002$). Precipitation had no impact on the number of flies per kg (Z = - 0.706; $p = .480$).

TABLE 3 Diversity index of host range according to fruit fly species and studied period

	Shannon		Species richness		Jackknife estimation		Dissimilarity		
	2001–2009	2018–2019	2001–2009	2018–2019	2001–2009	2018–2019	Bray	Sorensen	Common species between the two periods
B. dorsalis	–	2.69	–	30	–	39.0 ± 3	–	–	–
B. zonata	1.61	0.81	14	7	16.0 ± 1.4	12.0 ± 2.2	0.98	0.65	6/15
C. capitata	1.66	1.15	25	18	32.0 ± 2.6	29.0 ± 3.3	0.67	0.51	16/27
C. catoirii	0.11	0.85	5	3	7.0 ± 1.4	5.0 ± 1.4	0.99	0.50	3/5
C. quilicii	2.53	2.57	24	23	28.0 ± 2.0	29.0 ± 2.4	0.66	0.44	19/28
D. ciliatus	1.74	0.99	8	6	10.0 ± 1.4	9.0 ± 1.7	0.46	0.38	6/8
D. demmerezi	1.41	1.13	6	4	6.0 ± 0.0	5.0 ± 1.0	0.84	0.45	4/6
Z. cucurbitae	1.41	1.32	9	7	11.0 ± 1.4	11.0 ± 2.0	0.46	0.50	6/10
N. cyanescens	1.14	0.28	8	6	9.0 ± 1.0	7.0 ± 1.0	0.29	0.53	5/9

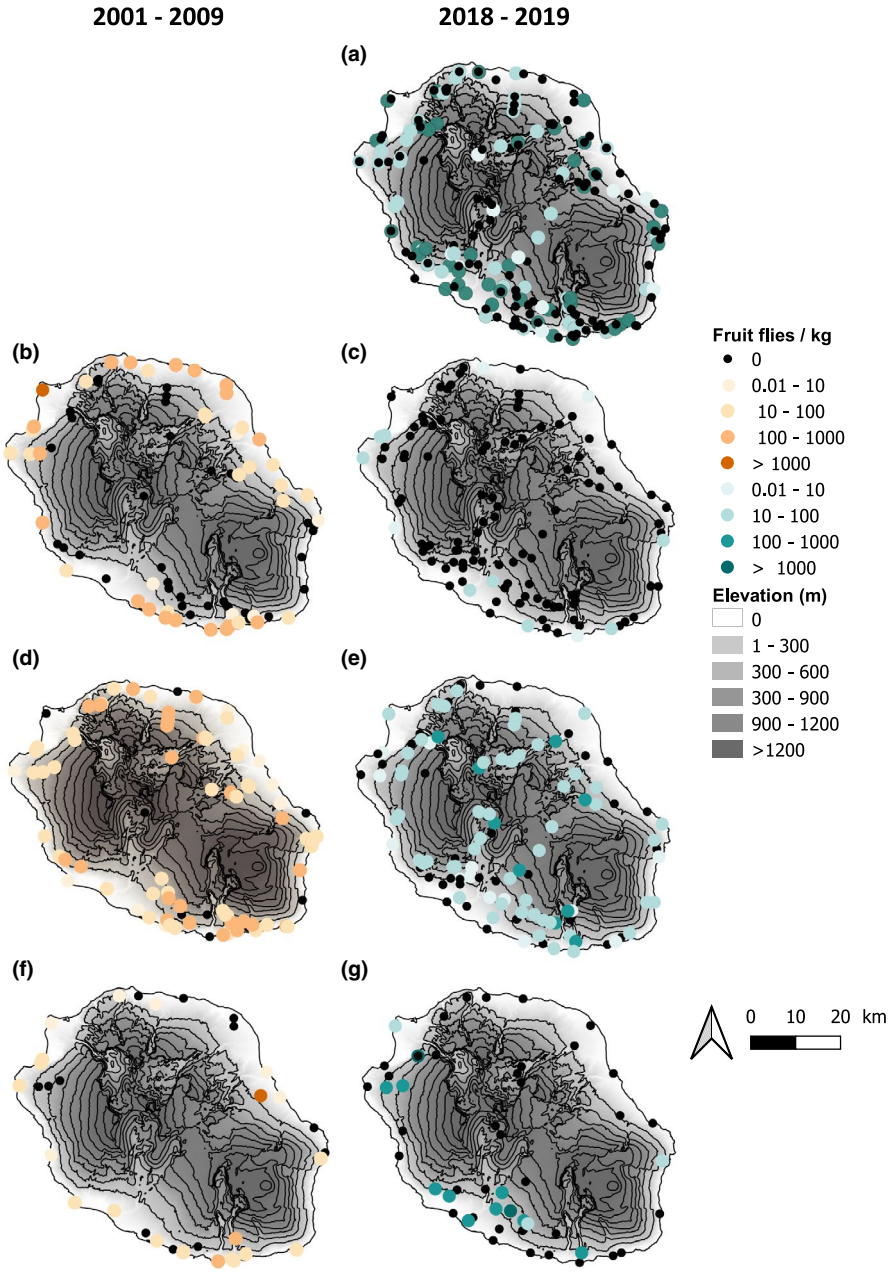

FIGURE 3 Distribution of samples infested by (a) *B. dorsalis*, (b, c) *B. zonata*, (d, e) *C. quilicii*, and (f, g) *C. capitata* during the 2001–2009 period (b, d, f) and 2018–2019 period (a, c, e, g) in La Réunion

3.3.2 | *Bactrocera zonata*

Bactrocera zonata was found on the coast in fruit harvested at low altitude between 0 and 600 m (Figure 3b,c). During the period 2001–2009, infestation rate significantly increased with temperature (Z = 3.495; *P* = < .001) and decreased with precipitation (*Z* = −2.251; *p* = .024). In 2001–2009, temperature had a positive effect on infestation rate (Z = 4.251; *p* < .001), but not precipitation (Z = −1.054; *p* = .292).

The niche equivalency test showed that the ecological niche was similar for the two studied periods (Niche overlap D = 0.61, I = 0.78, P_D = 0.06, P_I = 0.06, Figure 4b).

3.3.3 | *Ceratitis quilicii*

Ceratitis quilicii was present throughout the island and found in fruit harvested between 0 and 1,580 m altitude (Figure 3d,e). During the period 2001–2009, infestation rate significantly decreased with temperature (Z = −3.472; *p* < .001) and precipitation (Z = −2.216; *p* = .027). In 2001–2009, temperature had a negative effect on infestation rate (*Z* = −2.835; *p* = .004), but not precipitation (*Z* = −1.150; *p* = .250).

The niche equivalency test showed that the ecological niche was significantly different between the two studied periods (Niche overlap D = 0.51, I = 0.67, p_D = .35, p_I < .001). For the second sample period, *C. capitata* was less present in sites with higher temperatures (lower altitude) than for the first period (Figure 4c).

3.3.4 | *Ceratitis capitata*

Ceratitis capitata was more frequent in the west of the island and found in fruit harvested between 0 and 850 m altitude (Figure 3f, g). During the period 2001–2009, temperature (Z = 0.084; *p* = .933) and precipitation (*Z* = −0.834; *p* = .404) had no significant impact on infestation rate. In 2001–2009, precipitation had a negative effect on the infestation rate (*Z* = −1.999; *p* = .046), but not temperature (*Z* = −0.294; *p* = .768).

The niche equivalency tests showed that the ecological niche differed significantly between the two studied periods (Niche overlap D = 0.24, I = 0.034, p_D = <.001, p_I < .001, Figure 4). For the second sampling period, *C. capitata* was found in sites with lower precipitation and temperature than for the first period (Figure 4e).

3.3.5 | *Ceratitis catoirii*

Ceratitis catoirii was found in the north and south of the island in fruit harvested between 0 and 760 m altitude. There were not enough data to study the preference and niche modification of this rare endemic species (Figure 4d).

4 | DISCUSSION

One and two years after the *Bactrocera dorsalis* invasion, respectively, we observed a shift in the host range and spatial distribution of the established species. In the case of specialist species, which shared few host plant species with *B. dorsalis*, no significant change in host range was observed. On the contrary, generalist species such as *B. zonata*, *C. quilicii* and *C. capitata* modified their host range (diversity and proportion) and we observed a shift in their climatic niches.

4.1 | Host range of *B. dorsalis*

Our results confirm the generalist character of *B. dorsalis* in La Réunion. Of the 112 species tested, 52 were infested by *B. dorsalis* belonging to 23 families. In La Réunion, these species' primary

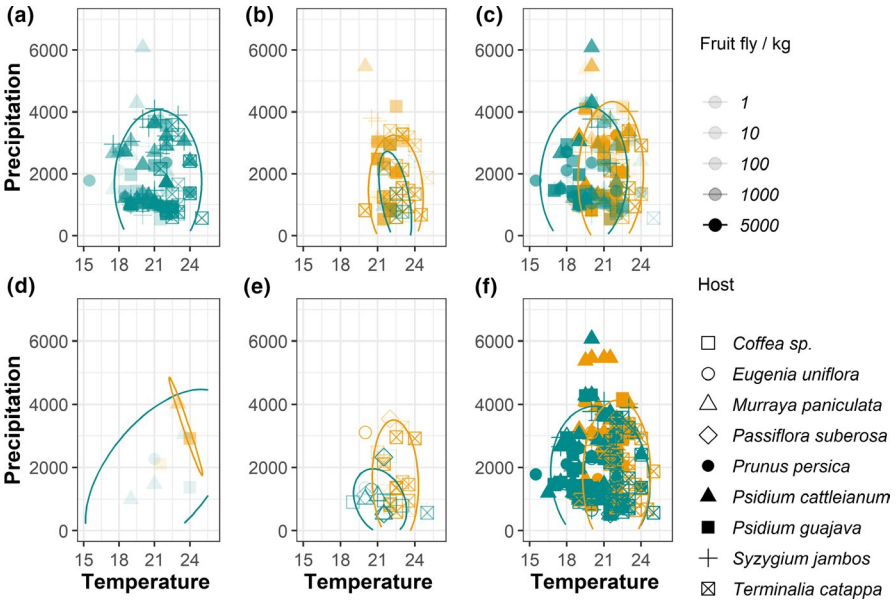

FIGURE 4 Mean of precipitation and temperature of sample sites collected in 2001–2009 and 2018–2019. Samples were infested by (a) *B. dorsalis*, (b) *B. zonata*, (c) *C. quilicii*, (d) *C. catoirii* and (e) *C. capitata*. All samples are represented in f) including uninfested fruits. Orange points correspond to the fruits collected in 2001–2009 and green points to fruits collected in 2018–2019

host plants (as a function of number of infested fruit, infestation rate measured by number of fruit flies per kg and abundance) were *Mangifera indica*, *Terminalia catappa*, *Syzygium jambos*, *Psidium cattleianum* and *Psidium guajava*. These plant species are regularly cited as essential hosts for this invasive species in different sites (Goergen, Vayssières, Gnanvossou, & Tindo, 2011). Their nutritional value maximizes larval development and survival in generalist species (Hafsi et al., 2016).

The invasion of *B. dorsalis* considerably increased the impact of fruit flies on agriculture in La Réunion because it infested new plant species not previously affected by the established species. These include *Ananas comosus*, *Hylocereus undatus*, *Litchi chinensis* or *Musa* sp. In addition, after the invasion, an increase in the number of infestation rates on *M. indica* was also observed.

Bactrocera dorsalis infestations were also observed on some cultivated Curcurbitaceae and Solanaceae species, such as *Momordica charantia*, *Sechium edule*, *Solanum betaceum* and *Solanum lycopersicum*, but to a lesser extent. Similar results showing low *B. dorsalis* infestation on these plants have also been recorded in other studies (Clarke et al., 2005; Goergen et al., 2011). Several factors could explain the relatively low infestation rates observed in these plant species, for example, female preference for oviposition, less efficient larval development or interspecific interactions. The specialist species (*Z. cucurbitae*, *D. ciliatus*, *D. demmerezi* and *N. cyanescens*) were found to infest a high proportion of Cucurbitaceae and Solanaceae fruit. They may have had direct interactions with the generalist species and, thus, may have been in direct competition for access to resources.

In addition to cultivated species, many wild species were infested by *B. dorsalis*. Both invasive species (for example, *P. catlleianum* or *S. jambos*) and endemic species (for example, *Aphloia theiformis* or *Ficus lateriflora*) were affected. Wild and cultivated host plants (in orchards or gardens) cover a large part of the island. The subtropical climate means that fruiting periods overlap the whole year round (Quilici & Jeuffrault, 2001). Wild species could potentially serve as reservoir hosts, which would allow fruit fly populations to persist in space and time, where or when the preferred plant host species are not available. These results reveal the importance of monitoring non-cultivated hosts when control strategies are developed for a particular fruit crop.

4.2 | Host range shift

Changes in the host range of established species have been observed in different ways. *Ceratitis* species had the same host plant diversity in 2018–2019. A decline in the host plant range of these species and reduced infestation rates had already been observed on mango, guava and Indian almond species after the arrival of *B. zonata* (Charlery de la Masselière et al., 2017). Therefore, the *Ceratitis* species were not fundamentally impacted by the invasion of *B. dorsalis* with regard to these host plants. Nevertheless, we observed differences in host composition for *C. quilicii* between the two periods studied. In addition, *C. capitata* became rarer in some plants, which had previously been major hosts, such as *Coffea* sp., *Mimusops elengi* and *Pithecellobium dulce*. These results are in accordance with other studies showing that invasive *Bactrocera* species can displace *Ceratitis* species from their preferred host plants (Duyck, Sterlin, et al., 2004; Ekesi, Mohamed, & De Meyer, 2016; Mwatawala et al., 2009a, 2009b). For example, *B. zonata* previously impacted the host range of *Ceratitis* species in La Réunion (Charlery de la Masselière et al., 2017); *B. dorsalis* displaced *C. cosyra* in Kenya (Ekesi et al., 2009) and *C. capitata* in Hawaii (Keiser et al., 1974), and became the predominant fruit fly pest of mango and guava in both countries. Our findings reveal two different types of response for *Ceratitis* species: *C. capitata* found an ecological refuge in host plants with small berries rarely infested by *B. dorsalis*, such as *Murraya paniculata* and *Passiflora suberosa*, while the *C. quilicii* host range largely overlaps that of *B. dorsalis*. This overlap is also illustrated by the high proportion of co-infestation between *B. dorsalis* and *C. quilicii* (68% of co-infested fruits).

Bactrocera zonata suffered a significant decrease in host species diversity and infestation rates. Two years after the *B. dorsalis* invasion, this species was very rare in all fruit samples collected. The competitive superiority of *B. dorsalis* is not surprising. In 2004, this species was already ranked as one of the top invaders and competitors among tephritid species (Duyck, et al., 2004). *Bactrocera dorsalis* has already caused the competitive displacement of other *Bactrocera species*, such as *B. tryoni*, *B. kirki* and *B. perfusca* in French Polynesia (Allwood & Drew, 1997; Leblanc & Putoa, 2000). Many researchers have demonstrated that an invader is competitively superior to the native or established species that it displaces (Duyck, Sterlin, et al., 2004; Reitz & Trumble, 2002). The intensity of the *B. dorsalis* invasion on the *B. zonata* population and its almost immediate impact were unexpected. Our results suggest that *B. zonata* may even be suffering from a process of competitive exclusion. In the literature, competitive exclusion is rarer than displacement (DeBach, 1966). In fruit flies, the only case of exclusion was reported for *C. catoirii* in Mauritius because of pressure from successive invasions of different species over the years (Duyck, Sterlin, et al., 2004). *Bactrocera zonata* has proven to be more sensitive than *Ceratitis* species to the invasion of *B. dorsalis*. One hypothesis could be that these closely related species suffered from greater competition because their niches were too similar. For a stable coexistence, species require different niches. Species that are ecologically too similar cannot coexist (Burns & Strauss, 2011; Macarthur & Levins, 1967; Peterson et al., 2013).

4.3 | Climatic niche shift

In our study, in addition to the host range shift, we observed a shift in the climatic niches after the *B. dorsalis* invasion. *Ceratitis quilicii* and *C. capitata* were less present at low altitude (higher temperature) and *C. capitata* was less present in the east of the island (higher humidity) following the *B. dorsalis* invasion. Similar niche partitioning associated with the *B. dorsalis* invasion was observed in Eastern Central Tanzania, where *C. rosa* became predominant at a higher

elevation (Geurts, Mwatawala, & De Meyer, 2012) and in Hawaii, where *C. capitata* populations were only maintained in peach and other fruit at high elevations (Keiser et al., 1974), while *B. dorsalis* was dominant in lowlands.

These results seem to demonstrate that established species are found in areas where they perform better (i.e. climatic optimum). They avoid areas colonized by *B. dorsalis*. *Bactrocera dorsalis* has an extensive ecological niche, both in terms of temperature and precipitation. Its niche (from 2018–2019 data) overlaps with that of other established species observed prior to 2009. Nevertheless, data collected showed a higher infestation rate in lowlands, corresponding to the optimum temperature for larval development, which is between 25°C and 30°C (Rwomushana, Ekesi, Ogol, & Gordon, 2008). *Ceratitis capitata* was less abundant in humid and warm areas of the island after the *B. dorsalis* invasions. Duyck and Quilici (2006) showed that this species is more adapted to a dry climate than other *Ceratitis* species. It can tolerate all temperatures between 15 and 30°C, although it develops more slowly than *C. quilicii* in lower temperatures. The infestation rate of *C. quilicii* decreased at low altitude after the invasion of *B. dorsalis*. This appears to be consistent with the fact that this species has a higher tolerance to low temperatures; its temperature threshold for larval development is 3.1°C (Duyck & Quilici, 2006). Thus, this observed shift could be due to niche-dependent competition, whereby each species becomes dominant in its optimum environment. Numerous models have shown that the environment has a considerable impact on the outcome of competition and tends to shift the balance in favour of one of the species (Snyder, 2008; Velázquez, Garrahan, & Eichhorn, 2014). Climatic niche displacement was probably one parameter that allowed the coexistence of *B. dorsalis* and the two *Ceratitis* species.

Bactrocera zonata has a climatic niche similar to that of *B. dorsalis* with an optimal development temperature between 25°C and 30°C (De Villiers et al., 2015; Duyck, Sterlin, et al., 2004; Ni et al., 2012). However, *B. zonata* is more sensitive to cold than the other two species, with a 12.6°C temperature threshold for larval development (Duyck & Quilici, 2006; Duyck, Sterlin, et al., 2004). In La Réunion, this species probably did not have the opportunity to escape from *B. dorsalis* at higher altitudes.

4.4 | The competitive displacement

Although we have no direct evidence of the impact of *B. dorsalis* on other species, we have a large amount of evidence regarding the competitive displacement induced by *B. dorsalis* on other established species. Before *B. dorsalis* was introduced in La Réunion, the coexistence of tephritid species was linked to the differentiation of climatic niche and host range, as demonstrated in studies by Duyck and colleagues (Duyck et al., 2008; Duyck & Quilici, 2006). However, the invasion of *B. dorsalis* affected this balance. We have shown that the coexistence between *B. dorsalis* and *C. quilicii* was possible because the species have a different response to temperature; that is, *C. quilicii* demonstrates a niche shift to a higher altitude than *B. dorsalis*. The coexistence of *C. capitata* with *B. dorsalis* and the other resident species was possible because of its ability to develop at a lower temperature (high altitude) and to exploit fruit species that are not host to other fruit fly species.

Bactrocera zonata and *B. dorsalis* have similar ecological requirements for climatic and host range. Both species prefer high temperatures and have a similar range of host plants, such as mango, Indian almond or guava. In La Réunion, the coexistence of *B. zonata* with *B. dorsalis* seems to be compromised (DeBach, 1966; Hardin, 1960). However, other studies showed that the coexistence of these two species is possible in other parts of the world, including non-native areas like Sudan (Agarwal et al., 1999; Mahmoud et al., 2020). According to climatic models, *B. zonata* seems a little less sensitive to dry stress than *B. dorsalis* (De Villiers et al., 2015; Ni et al., 2012). We suppose that differences in tolerance allow the coexistence of *B. dorsalis* and *B. zonata* within the limits of climatic suitability for *B. dorsalis*.

Many parameters could influence the competitive outcomes. For example, previous studies have shown that oviposition competition occurs between adult females. Liu et al. (2017) showed that *B. dorsalis* species has a clear advantage when competing with *C. capitata* for egg-laying. Aggressive behaviour has been observed in some fruit fly species, including *B. dorsalis*. Females are reported to defend their oviposition sites from other females (Benelli, 2014; Shelly, 1999) and may be the cause of agonistic interference competition. In addition, competition between females for egg-laying sites could be an issue if *B. dorsalis* has a greater capacity for locating or exploiting the resource or if *B. dorsalis* uses the resource at an earlier stage than other fruit fly species (Rwomushana et al., 2009). In the case of co-infestation of the same fruit, interactions between larvae could create interference or competition (Duyck et al., 2008; Rwomushana et al., 2009; Shen et al., 2014). In larval competition, the short duration of larval development of *Bactrocera* species appears to be an advantage (Duyck, David, & Quilici, 2007).

Other mechanisms could promote coexistence or competitive displacement, such as apparent competition. This occurs when a natural enemy increases in number or becomes more efficient at attacking a given species in the presence of a third species (Holt, 1977). Some cases of niche shift, which were interpreted as competitive displacement, may actually involve apparent competition (David et al., 2017). In La Réunion, generalist species share the same parasitoid, *Fopius arisanus*. This parasitoid could have a different effect on fruit fly species that coexist in the same biotope (Rousse, Gourdon, & Quilici, 2006).

5 | CONCLUSION

Our results have implications for control programmes. Integrated information on interaction networks, including competition, is a necessary step for identifying empty niches and modelling potential species distribution. On the basis of the hypothesis of

hierarchical competition in Tephritideae, it would be interesting to determine whether or not the presence of *B. dorsalis* limits the invasion by *B. zonata*. In addition, eradication programmes may have unexpected impacts on non-target species, especially through indirect effects. For example, local eradication of *B. dorsalis* could lead to an increase in *B. zonata* populations because of reduced competition.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available in the CIRAD dataverse: https://dataverse.cirad.fr/dataset.xhtml?persistentId=doi:10.18167/DVN1/RMQQFZ.

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REFERENCES

Agarwal, M. L., Kumar, P., & Kumar, V. (1999). Population suppression of *Bactrocera dorsalis* (hendel) by *Bactrocera zonata* (Saunders) (Diptera: Tephritidae) in North Bihar. *Shashpa*, *6*, 189–191.

Allwood, A. J., & Drew, R. A. I. (1997). *Management of fruit flies in the Pacific. A regional symposium*. Australian Centre for International Agricultural Research (Australia).

Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: A synthesis. *Ecology Letters*, *6*, 1109–1122.

Badii, K. B., Billah, M. K., Afreh-Nuamah, K., & Obeng-Ofori, D. (2015). Species composition and host range of fruit-infesting flies (Diptera: Tephritidae) in northern Ghana. *International Journal of Tropical Insect Science*, *35*, 137–151.

Benelli, G. (2014). Aggression in Tephritidae flies: Where, when, why? Future directions for research in integrated pest management. *Insects*, *6*, 38–53.

Billah, M. K., & Ekesi, S. (2006). *A field guide to the management of economically important tephritid fruit flies in Africa*. ICIPE Science Press.

Blonder, B. (2018). Hypervolume concepts in niche- and trait-based ecology. *Ecography*, *41*, 1441–1455. https://doi.org/10.1111/ecog.03187

Boinahadji, A. K., Coly, E. V., Dieng, E. O., Diome, T., & Sembene, P. M. (2019). Interactions between the oriental fruit fly *Bactrocera dorsalis* (Diptera, Tephritidae) and its host plants range in the Niayes area in Senegal. *Journal of Entomology and Zoology Studies*, *7*, 855–864.

Bray, J. R., & Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, *27*, 325–349. https://doi.org/10.2307/1942268

Broennimann, O., Fitzpatrick, M. C., Pearman, P. B., Petitpierre, B., Pellissier, L., Yoccoz, N. G., Thuiller, W., Fortin, M.-J., Randin, C., Zimmermann, N. E., Graham, C. H., & Guisan, A. (2012). Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*, *21*, 481–497. https://doi.org/10.1111/j.1466-8238.2011.00698.x

Burns, J. H., & Strauss, S. Y. (2011). More closely related species are more ecologically similar in an experimental test. *Proceedings of the National Academy of Sciences*, *108*, 5302–5307. https://doi.org/10.1073/pnas.1013003108

Charlery de la Masselière, M., Ravigné, V., Facon, B., Lefeuvre, P., Massol, F., Quilici, S., & Duyck, P.-F. (2017). Changes in phytophagous insect host ranges following the invasion of their community : Long-term data for fruit flies. *Ecology and Evolution*, *7*, 5181–5190.

Clarke, A. R., Armstrong, K. F., Carmichael, A. E., Milne, J. R., Raghu, S., Roderick, G. K., & Yeates, D. K. (2005). Invasive phytophagous pests arising through a recent tropical evolutionary radiation: The *Bactrocera dorsalis* complex of fruit flies. *Annual Review of Entomology*, *50*, 293–319.

Cola, V. D., Broennimann, O., Petitpierre, B., Breiner, F. T., D'Amen, M., Randin, C., & Guisan, A. (2017). Ecospat : An R package to support spatial analyses and modeling of species niches and distributions. *Ecography*, *40*, 774–787.

Colautti, R. I., Bailey, S. A., van Overdijk, C. D. A., Amundsen, K., & MacIsaac, H. J. (2006). Characterised and projected costs of nonindigenous species in Canada. *Biological Invasions*, *8*, 45–59. https://doi.org/10.1007/s10530-005-0236-y

Czárán, T. (1991). Coexistence of competing populations along an environmental gradient: A simulation study. E. Feoli & L. Orlóci *Computer assisted vegetation analysis* (pp. 317–324). Dordrecht: Springer.

David, P., Thébault, E., Anneville, O., Duyck, P.-F., Chapuis, E., & Loeuille, N. (2017). Impacts of invasive species on food webs :a review of empirical data. D.A. Bohan A.J. Dumbrell & F. Massol In *Advances in Ecological Research* (Vol. *56*, p. 1–60). Academic Press.

De Meyer, M., Mohamed, S., & White, I. M. (2014). Invasive fruit fly pests in Africa: A diagnostic tool and information reference for the four Asian species of fruit fly (Diptera, Tephritidae) that have become accidentally established as pests in Africa, including the Indian Ocean Islands. Online at: http://www.africamuseum.be/fruitfly/AfroAsia.htm (accessed 19 August 2012).

De Meyer, M., Quilici, S., Franck, A., Chadhouliati, A. C., Issimaila, M. A., Youssoufa, M. A., & White, I. M. (2012). Records of frugivorous fruit flies (Diptera: Tephritidae: Dacini) from the Comoro archipelago. *African Invertebrates*, *53*, 69–77.

De Villiers, M., Hattingh, V., Kriticos, D. J., Brunel, S., Vayssières, J.-F., Sinzogan, A., & Abdelgader, H. (2015). The potential distribution of *Bactrocera dorsalis* : Considering phenology and irrigation patterns. *Bulletin of Entomological Research*, *106*, 19–33.

DeBach, P. (1966). The competitive displacement and coexistence principles. *Annual Review of Entomology*, *11*, 183–212. https://doi.org/10.1146/annurev.en.11.010166.001151

Denno, R. F., McClure, M. S., & Ott, J. R. (1995). Interspecific interactions in phytophagous insects: Competition reexamined and resurrected. *Annual Review of Entomology*, *40*, 297–331.

Duyck, P.-F., David, P., Pavoine, S., & Quilici, S. (2008). Can host-range allow niche differentiation of invasive polyphagous fruit flies (Diptera: Tephritidae) in La Réunion? *Ecological Entomology*, *33*, 439–452.

Duyck, P.-F., David, P., & Quilici, S. (2004). A review of relationships between interspecific competition and invasions in fruit flies (Diptera: Tephritidae). *Ecological Entomology*, *29*, 511–520.

Duyck, P.-F., David, P., & Quilici, S. (2006). Climatic niche partitioning following successive invasions by fruit flies in La

Réunion. *Journal of Animal Ecology*, *75*, 518–526. https://doi.org/10.1111/j.1365-2656.2006.01072.x

Duyck, P.-F., David, P., & Quilici, S. (2007). Can more K-selected species be better invaders? A case study of fruit flies in La Réunion. *Diversity and Distributions*, *13*, 535–543. https://doi.org/10.1111/j.1472-4642.2007.00360.x

Duyck, P.-F., & Quilici, S. (2002). Survival and development of different life stages of three *Ceratitis*spp. (Diptera: Tephritidae) reared at five constant temperatures. *Bulletin of Entomological Research*, *92*, 461–469.

Duyck, P.-F., Sterlin, J. F., & Quilici, S. (2004). Survival and development of different life stages of *Bactrocera zonata* (Diptera: Tephritidae) reared at five constant temperatures compared to other fruit fly species. *Bulletin of Entomological Research*, *94*, 89–93.

Ekesi, S., Billah, M. K., Nderitu, P. W., Lux, S. A., & Rwomushana, I. (2009). Evidence for competitive displacement of *Ceratitis cosyra* by the invasive fruit fly *Bactrocera invadens* (Diptera : Tephritidae) on mango and mechanisms contributing to the displacement. *Journal of Economic Entomology*, *102*, 981–991.

Ekesi, S., Mohamed, S. A., De Meyer, M. (Éds.) (2016). *Fruit fly research and development in Africa—Towards a sustainable management strategy to improve horticulture*. Springer.

Eskafi, F. M., & Fernandez, A. (1990). Larval–pupal mortality of Mediterranean fruit fly (Diptera: Tephritidae) from interaction of soil, moisture, and temperature. *Environmental Entomology*, *19*, 1666–1670.

Fadlelmula, A. A., & Ali, E. B. M. (2014). Fruit fly species, their distribution, host range and seasonal abundance in blue nile state, Sudan. *Persian Gulf Crop Protection*, *3*, 17–24.

FAO, IAEA (2019). In W. R. Enkerlin, J. Reyes, & G.. Ortiz (Éds.), *Fruit Sampling Guidelines for Area-Wide Fruit Fly Programmes*, (1–38). Vienna: FAO.

Geurts, K., Mwatawala, M., & De Meyer, M. (2012). Indigenous and invasive fruit fly diversity along an altitudinal transect in Eastern Central Tanzania. *Journal of Insect Science*, *12*, 1–18. https://doi.org/10.1673/031.012.1201

Geurts, K., Mwatawala, M. W., & De Meyer, M. (2014). Dominance of an invasive fruit fly species, *Bactrocera invadens*, along an altitudinal transect in Morogoro, Eastern Central Tanzania. *Bulletin of Entomological Research*, *104*, 288–294.

Goergen, G., Vayssières, J.-F., Gnanvossou, D., & Tindo, M. (2011). *Bactrocera invadens* (Diptera: Tephritidae), a new invasive fruit fly pest for the Afrotropical region: Host plant range and distribution in West and Central Africa. *Environmental Entomology*, *40*, 844–854.

Gomina, M. (2015). *Contribution a la connaissance des mouches des fruits (Diptera : Tephritidae) et de leurs parasitoides au sud du Togo* (PhD Thesis). Université de Lome.

Grünberger, O. (1989). *Étude géochimique et isotopique de l'infiltration sous climat tropical contrasté, Massif du piton des Neiges, île de la Réunion* (PhD Thesis). Université Paris Sud, Paris.

Hafsi, A., Facon, B., Ravigné, V., Chiroleu, F., Quilici, S., Chermiti, B., & Duyck, P.-F. (2016). Host plant range of a fruit fly community (Diptera: Tephritidae): Does fruit composition influence larval performance? *BMC Ecology*, *16*, 40.

Hardin, G. (1960). The competitive exclusion principle. *Science*, *131*, 1292–1297. https://doi.org/10.1126/science.131.3409.1292

Hassani, I. S. S. A. M. (2017). *Etude écologique des mouches des fruits (Diptera : Tephritidae) nuisibles aux cultures fruitières aux Comores* (PhD Thesis). : Université de La Réunion, Université D'Antananarivo.

Hassani, I. M., Raveloson-Ravaomanarivo, L. H., Delatte, H., Chiroleu, F., Allibert, A., Nouhou, S., & Duyck, P.-F. (2016). Invasion by *Bactrocera dorsalis* and niche partitioning among tephritid species in Comoros. *Bulletin of Entomological Research*, *106*, 749–758.

Holt, R. D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, *12*, 197–229. https://doi.org/10.1016/0040-5809(77)90042-9

Isabirye, B. E., Akol, A. M., Muyinza, H., Masembe, C., Rwomushana, I., & Nankinga, C. K. (2016). Fruit fly (Diptera: Tephritidae) host status and relative infestation of selected mango cultivars in three agro ecological zones in Uganda. *International Journal of Fruit Science*, *16*, 23–41.

Iwaizumi, R. (2004). Species and host record of the *Bactrocera dorsalis* complex (Diptera: Tephritidae) detected by the plant quarantine of Japan. *Applied Entomology and Zoology*, *39*, 327–333.

Joomaye, A., Price, N. S., & Stonehouse, J. M. (2000). Quarantine pest risk analysis of fruit flies in the Indian Ocean : The case of Bactrocera zonata. Proceedings of the Indian Ocean Commission, Regional Fruit Fly Symposium, Flic en Flac, Mauritius, 5th–9th June, 2000, 179–183. Indian Ocean Commission.

José, L., Cugala, D., & Santos, L. (2013). Assessment of invasive fruit fly fruit infestation and damage in Cabo Delgado Province, Northern Mozambique. *African Crop Science Journal*, *21*, 21–28.

Keiser, I., Kobayashi, R. M., Miyashita, D. H., Harris, E. J., Schneider, E. L., & Chambers, D. L. (1974). Suppression of mediterranean fruit flies by oriental fruit flies in mixed infestations in guava. *Journal of Economic Entomology*, *67*, 355–360.

Leblanc, L., & Putoa, R. (2000). *Les mouches des fruits de la Polynésie française et des îles Pitcairn*. : Service de la Protection des Végétaux, Secretariat Général de la communauté du Pacifique.

Leblanc, L., Vueti, E. T., & Allwood, A. J. (2013). Host plant records for fruit flies (Diptera: Tephritidae: Dacini) in the Pacific Islands: 2. Infestation statistics on economic hosts. *Proceedings of the Hawaiian Entomological Society*, *45*, 83–117.

Leblanc, L., Vueti, E. T., Drew, R. A., & Allwood, A. J. (2012). Host plant records for fruit flies (Diptera: Tephritidae: Dacini) in the Pacific Islands. *Proceedings of the Hawaiian Entomological Society*, *44*, 11–53.

Liu, H., Zhang, C., Hou, B.-H., Ou-Yang, G.-C., & Ma, J. (2017). Interspecific competition between *Ceratitis capitata* and two *Bactrocera* spp. (Diptera : Tephritidae) evaluated via adult behavioral interference under laboratory conditions. *Journal of Economic Entomology*, *110*, 1145–1155.

Lux, S. A., Copeland, R. S., White, I. M., Manrakhan, A., & Billah, M. K. (2003). A new invasive fruit fly species from the *Bactrocera dorsalis* (Hendel) group detected in East Africa. *International Journal of Tropical Insect Science*, *23*, 355–361. https://doi.org/10.1017/S1742758400012420X

Macarthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, *101*, 377–385. https://doi.org/10.1086/282505

Mahmoud, A. A. (2016). Effect of temperature on the development and survival of immature stages of the peach fruit fly, *Bactrocera zonata* (Saunders) (Diptera: Tephritidae). *African Journal of Agricultural Research*, *11*, 3375–3381.

Mahmoud, M. E. E., Mohamed, S. A., Ndlela, S., Azrag, A. G. A., Khamis, F. M., Bashir, M. A. E., & Ekesi, S. (2020). Distribution, relative abundance, and level of infestation of the invasive peach fruit fly *Bactrocera zonata* (Saunders) (Diptera: Tephritidae) and its associated natural enemies in Sudan. *Phytoparasitica*, *48*, 589–605.

Mauremootoo, J. R., Pandoo, S., Bachraz, V., Buldowoo, I., & Cole, N. C. (2019). Invasive species management in Mauritius : From the reactive to the proactive–the National Invasive Species Management Strategy and its implementation. In C. R. Veitch, M. N. Clout, A. R. Martin, J. C. Russell, & C. J. West (Eds.), *Island invasives: Scaling up to meet the challenge. Proceedings of the international conference on island invasives 2017* (pp. 503–509). IUCN, International Union for Conservation of Nature.

McQuate, G. T. (2010). Tephritid fruit fly populations in a dragonfruit orchard in Hawaii : Border plant use and infestation rate. *Proceedings of the Hawaiian Entomological Society*, *42*, 41–48.

Millennium Ecosystem Assessment (Program) (Éd.) (2005). *Ecosystems and human well-being: Synthesis*. Island Press.

Murphy, G. E., & Romanuk, T. N. (2014). A meta-analysis of declines in local species richness from human disturbances. *Ecology and Evolution*, *4*, 91–103. https://doi.org/10.1002/ece3.909

Musseau, C., Vincenzi, S., Jesenšek, D., Boulêtreau, S., Santoul, F., & Crivelli, A. J. (2016). Sympatry with the devil? Niche-based Approach Explains the Mechanisms Allowing Coexistence of Native and non-native Salmonids. *bioRxiv*, 068171.

Mwatawala, M. W., De Meyer, M., Makundi, R. H., & Maerere, A. P. (2006). Seasonality and host utilization of the invasive fruit fly, *Bactrocera invadens* (Dipt., Tephritidae) in central Tanzania. *Journal of Applied Entomology*, *130*, 530–537.

Mwatawala, M. W., De Meyer, M., Makundi, R. H., & Maerere, A. P. (2009a). An overview of Bactrocera (Diptera: Tephritidae) invasions and their speculated dominancy over native fruit fly species in Tanzania.*Journal of Entomology*, *6*, 18–27.

Mwatawala, M. W., De Meyer, M., Makundi, R. H., & Maerere, A. P. (2009b). Host range and distribution of fruit-infesting pestiferous fruit flies (Diptera, Tephritidae) in selected areas of Central Tanzania. *Bulletin of Entomological Research*, *99*, 629–641. https://doi.org/10.1017/S0007485309006695

Mziray, H. A., Makundi, R. H., Mwatawala, M., Maerere, A., & De Meyer, M. (2010). Host use of *Bactrocera latifrons*, a new invasive tephritid species in Tanzania. *Journal of Economic Entomology*, *103*, 70–76.

N'Dépo, O. R., Hala, N. F., Gnago, A., Allou, K., Kouassi, K. P., Vayssières, J.-F., & De Meyer, M. (2010). Inventaire des mouches des fruits de trois régions agro-écologiques et des plantes-hôtes associées à l'espèce nouvelle, *Bactrocera* (*Bactrocera invadens* Drew et al)(Diptera : Tephritidae) en Côte-d'Ivoire. *European Journal of Scientific Research*. *46*, 62–72.

N'Dépo, O. R., My, M., & NI, Y. (2019). Host plants associated with tephritidae in Côte d'Ivoire and discovery of a new fruit fly species: *Dasus longistylus*. *Journal of Entomology and Zoology Studies*, *7*, 1301–1308.

Ndiaye, O., Vayssieres, J.-F., Rey, J. Y., Ndiaye, S., Diedhiou, P. M., Ba, C. T., & Diatta, P. (2012). Seasonality and range of fruit fly (Diptera: Tephritidae) host plants in orchards in Niayes and the Thiès Plateau (Senegal). *Fruits*, *67*, 311–331.

Ni, W. L., Li, Z. H., Chen, H. J., Wan, F. H., Qu, W. W., Zhang, Z., & Kriticos, D. J. (2012). Including climate change in pest risk assessment : The peach fruit fly, *Bactrocera zonata* (Diptera: Tephritidae). *Bulletin of Entomological Research*, *102*, 173–183.

Olson, L. J. (2006). The economics of terrestrial invasive species : A review of the literature. *Agricultural and Resource Economics Review*, *35*, 178–194.

Peterson, M. L., Rice, K. J., & Sexton, J. P. (2013). Niche partitioning between close relatives suggests trade-offs between adaptation to local environments and competition. *Ecology and Evolution*, *3*, 512–522. https://doi.org/10.1002/ece3.462

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T., & Tsomondo, T. (2001). Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems & Environment*, *84*, 1–20. https://doi.org/10.1016/S0167-8809(00)00178-X

Pimentel, D., Zuniga, R., & Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, *52*, 273–288. https://doi.org/10.1016/j.ecolecon.2004.10.002

Quilici, S., & Jeuffrault, E. (2001). *Plantes-hôtes des mouches des fruits : Maurice, Réunion, Seychelles (Programme Régional de Recherche Appliquée sur les Mouches des Fruits/Commission de l'Océan Indien)*. PRMF.

R Core Team (2019). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*, https://www.R-project.org/

Rattanapun, W. (2009). *Mango varietal preference and the effect of physiological changes during mango ripening on host utilisation by Bactrocera dorsalis (Hendel) (Diptera : Tephritidae)* (PhD Thesis). Kasetsart University.

Reitz, S. R., & Trumble, J. T. (2002). Competitive displacement among insects and arachnids. *Annual Review of Entomology*, *47*, 435–465. https://doi.org/10.1146/annurev.ento.47.091201.145227

Ricciardi, A., Hoopes, M. F., Marchetti, M. P., & Lockwood, J. L. (2013). Progress toward understanding the ecological impacts of non-native species. *Ecological Monographs*, *83*, 263–282. https://doi.org/10.1890/13-0183.1

Rousse, P., Gourdon, F., & Quilici, S. (2006). Host specificity of the egg pupal parasitoid *Fopius arisanus* (Hymenoptera : Braconidae) in La Reunion. *Biological Control*, *37*, 284–290.

Rwomushana, I., Ekesi, S., Gordon, I., & Ogol, C. K. P. O. (2008). Host plants and host plant preference studies for *Bactrocera invadens* (Diptera : Tephritidae) in Kenya, a new invasive fruit fly species in Africa. *Annals of the Entomological Society of America*, *101*, 331–340.

Rwomushana, I., Ekesi, S., Ogol, C. K. P. O., & Gordon, I. (2008). Effect of temperature on development and survival of immature stages of *Bactrocera invadens* (Diptera: Tephritidae). *Journal of Applied Entomology*, *132*, 832–839.

Rwomushana, I., Ekesi, S., Ogol, C. K. P. O., & Gordon, I. (2009). Mechanisms contributing to the competitive success of the invasive fruit fly *Bactrocera invadens* over the indigenous mango fruit fly, *Ceratitis cosyra* : The role of temperature and resource pre-emption. *Entomologia Experimentalis Et Applicata*, *133*, 27–37.

Shelly, T. E. (1999). Defense of oviposition sites by female oriental fruit flies (Diptera: Tephritidae). *The Florida Entomologist*, *82*, 339.

Shen, K., Hu, J., Wu, B., An, K., Zhang, J., Liu, J., & Zhang, R. (2014). Competitive interactions between immature stages of *Bactrocera cucurbitae* (Coquillett) and *Bactrocera tau* (Walker) (Diptera: Tephritidae) under laboratory conditions. *Neotropical Entomology*, *43*, 335–343.

Shoukry, A., & Hafez, M. (1979). Studies on the biology of the Mediterranean fruit fly *Ceratitis capitata*. *Entomologia Experimentalis Et Applicata*, *26*, 33–39. https://doi.org/10.1111/j.1570-7458.1979.tb02894.x

Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., & Vilà, M. (2013). Impacts of biological invasions : What's what and the way forward. *Trends in Ecology & Evolution*, *28*, 58–66.

Snyder, R. E. (2008). When does environmental variation most influence species coexistence? *Theoretical Ecology*, *1*, 129–139. https://doi.org/10.1007/s12080-008-0015-3

Sørensen, T. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. *Biologiske Skrifter /Kongelige Danske Videnskabernes Selskab*, *5*, 1–34.

Teruya, T. (1990). Effect of relative humidity during pupal maturation on subsequent adult eclosion and flight capability of the melon fly, *Dacus cucurbitae* Coquillett (Diptera: Tephritidae). *Applied Entomology and Zoology*, *25*, 521–523.

Theron, C. D., Manrakhan, A., & Weldon, C. W. (2017). Host use of the oriental fruit fly, *Bactrocera dorsalis* (Hendel)(Diptera : Tephritidae), in South Africa. *Journal of Applied Entomology*, *141*, 810–816.

Tilman, D., Mattson, M., & Langer, S. (1981). Competition and nutrient kinetics along a temperature gradient : An experimental test of a mechanistic approach to niche theory. *Limnology and Oceanography*, *26*, 1020–1033.

Vargas, R. I., Leblanc, L., Putoa, R., & Eitam, A. (2007). Impact of introduction of *Bactrocera dorsalis* (Diptera : Tephritidae) and

classical biological control releases of *Fopius arisanus* (hymenoptera : Braconidae) on economically important fruit flies in french polynesia. *Journal of Economic Entomology*, *100*, 670–679.

Vargas, R. I., Walsh, W. A., Jang, E. B., Armstrong, J. W., & Kanehisa, D. T. (1996). Survival and development of immature stages of four Hawaiian fruit flies (Diptera: Tephritidae) reared at five constant temperatures. *Annals of the Entomological Society of America*, *89*, 64–69.

Vayssières, J. F., Sinzogan, A., & Adandonon, A. (2009). *Range of cultivated and wild host plants of the main mango fruit fly species in Benin. leaflet no. 8*. Cotonou, Benin: Regional Fruit Fly Control Project in West Africa (WAFFI).

Velázquez, J., Garrahan, J. P., & Eichhorn, M. P. (2014). Spatial complementarity and the coexistence of species. *PLoS One*, *9*, e114979. https://doi.org/10.1371/journal.pone.0114979

Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., & Hulme, P. E. (2010). How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment*, *8*, 135–144. https://doi.org/10.1890/080083

Vila, M., & Weiner, J. (2004). Are invasive plant species better competitors than native plant species ? Evidence from pair-wise experiments. *Oikos*, *105*, 229–238.

White, I. M., De Meyer, M., & Stonehouse, J. (2000). A review of native and introduced fruit flies (Diptera, Tephritidae) in the Indian Ocean islands of Mauritius, Réunion, Rodrigues and Seychelles. *Proceedings of the Indian Ocean Commission, Regional Fruit Fly Symposium, Flic En Flac, Mauritius, 5th-9th June, 2000*, *15–21*.

White, I. M., & Elson-Harris, M. M. (1992). *Fruit flies of economic significance : Their identification and bionomics*. CAB International.

Yang, P., Carey, J. R., & Dowell, R. V. (1994). Temperature influences on the development and demography of *Bactrocera dorsalis* (Diptera: Tephritidae) in China. *Environmental Entomology*, *23*, 971–974.

Zeng, Y., Reddy, G. V. P., Li, Z., Qin, Y., Wang, Y., Pan, X., & Zhao, Z.-H. (2019). Global distribution and invasion pattern of oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae). *Journal of Applied Entomology*, *143*, 165–176.

BIOSKETCH

The research team works on the ecological dynamic in insular biotope. The team's work aims to improve knowledge of the biology, ecology and genetics of populations of arthropods of agricultural interest, to identify the structuring factors of plant and arthropod communities in agroecosystems or natural ecosystems. Tephritidae is one of the models of study followed for many years in La Reunion.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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